Rhamdia guasarensis (Siluriformes: Heptapteridae), a new species of cave catfish from the Sierra de Perijá, northwestern Venezuela

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Abstract.—*Rhamdia guasarensis* n. sp. is described from subterranean waters
in the Río Guasare drainage of northwestern Venezuela. The new species is
distinguished from congeners by its concave head profile; medially sutured
frontal bones; small, circular vestige of the anterior cranial fontanelle; and
troglomorphic characters such as absence of eyes and pigmentation, wide ce-
phalic laterosensory pores, and wide fossae of preoperculomandibular sensory
canal in preopercle and dentary. Cave catfish diversity in the Sierra de Perijá
region of Venezuela is reviewed and compared to cave catfish diversity else-
where in South America.

Resumen.—Se describe *Rhamdia guasarensis* sp. n. proveniente de aguas
subterráneas de la cuenca del Río Guasare en el noroccidente de Venezuela.
La nueva especie se diferencia de las restantes especies que conforman el
género por su perfil dorsal de la cabeza cóncavo; huesos frontales suturados
medialmente; fontanela craneal anterior reducida a un pequeño foramen cir-
cular; y caracteres troglomórficos tales como ausencia de ojos y pigmentación,
poros cefálicos latero sensoriales anchos, fosas ensanchadas del canal sensorial
preoperculomandibular en el preopérculo y dentario. La diversidad de bagres
cavernícolas de la Sierra de Perijá es revisada y comparada con la diversidad
de bagres cavernícolas de otras regiones de Suramérica.

The family Heptapteridae has invaded
and adapted to hypogean waters multiple
times. Among Neotropical catfish families,
heptapterids have the greatest diversity of
truly troglobitic taxa: *Phreatobius cister-
narum, Pimelodella kronei, Rhamdia lalu-
chensis, Rhamdia laticauda typhla, Rham-
dia macuspanensis, Rhamdia quelen urichi,
Rhamdia redelli,* and *Rhamdia zongolicen-
sis.* Trajano & Bockmann (2000) described
the ecology and behavior of *Taunayia* sp.,
a troglobitic catfish, inhabiting caves of
northeastern Brazil, but the species has not
been formally named. *Pimelodella spelea*

Trajano, Reis & Bichuette, 2004 is a re-
cently described troglophile without
marked specializations for hypogean life.
Taxonomic practice has shifted away from
assigning supra-specific rank to cave-dwell-
ing fishes solely on account of their trog-
lobitic adaptations. Among Heptapteridae,
the nominal monotypic genera *Caecorham-
dia, Caecorhamdella,* and *Typhlobagrus*
have long been treated as synonyms of
Rhamdia and *Pimelodella* respectively. Fur-
thermore, Silfvergrip (1996) synonymized
all cave populations of *Rhamdia* described
as separate species with *R. quelen* or *R.*

laticauda, both wide-ranging epigean species.

In this paper we describe a new troglobitic heptapterid species in the genus *Rhamdia.* Our placement of the new species is more a matter of convenience than firm phylogenetic resolution. *Rhamdia* is taxonomically complex. In the latest revision of the genus, Silfvergrip (1996) consolidated its approximately 100 nominal species into eight and he described three new species. In 1998, Weber & Wilkens described the blind species *R. macuspanensis,* and in 2003, Weber et al. described *Rhamdia laluchensis,* another troglobitic species from Mexico. In the most thorough phylogenetic study of Heptapteridae to date, Bockmann (1998) concluded that *Rhamdia* is nonmonophyletic but he did not attempt to resolve the genus into phylogenetically diagnosable units. As it stands, *Rhamdia* is a non-monophyletic assemblage of common fishes with an immense geographic distribution in South and Middle America from the lower Paraná Basin in Argentina to central México.

The new species, from a cave in the Sierra de Perijá region of northwestern Venezuela, is distinct both in its typical troglobitic specializations and other apomorphic features, but overall it is most similar to other *Rhamdia.* Discovering the relationships of the new species and, more generally, resolving the relationships of *Rhamdia* species are major problems quite beyond our present scope. Our immediate concern is to name and describe this previously unseen species that has a highly restricted distribution in a marginal and potentially fragile habitat. We comment also on the subterranean catfish fauna of the Perijá region.

Material and Methods

Morphometric measurements follow the criteria set out by Lundberg & McDade (1986) and Bockmann (1994). Terminology of cephalic laterosensory canals and branches follows Arratia & Huaquin's de-

scription of *Diplomystes* and *Nematogenys* (1995). However, our numbering of sensory pores in *Rhamdia* reflects anteroposterior or mesiolateral pore order, and does not imply individual homologies of pores among catfishes. All measurements were made on the left side of the specimens using a Mitutoyo digital, needlepoint caliper at a precision of 0.1 mm. For osteological observation one paratype (101.1 mm SL) was cleared and stained using the method of Taylor & Van Dyke (1985). A second paratype (93.4 mm SL) was radiographed. Only these two specimens were used for counts of vertebrae, branchiostegal rays, ribs, and pterygiophores. The vertebral count includes the first five vertebrae incorporated into the Weberian apparatus whereas the compound caudal centrum is counted as one. Institutional abbreviations follow Leviton et al. (1985). Other abbreviations are: SL—standard length, HL—head length, CS—cleared and stained skeletal preparation, alc—whole specimen preserved in alcohol.

Rhamdia guasarensis, new species
Figs. 1–4

Holotype.—MBUCV-V-29604: 106.8 mm SL; Surgencia del Tigre at 2.5 km W of Cerro Yolanda, Río Guasare basin, Sierra de Perijá, Estado Zulia, Venezuela (10°52′53″N, 72°30′03″W). Elevation 200 m asl; collected by J. Lagarde, 3 April 1999.

Paratypes.—All collected with the holotype: MBUCV-V-29622, two specimens, 87.2–101.1 mm SL, the second cleared and stained; ANSP 179878, one specimen, 93.4 mm SL.

Diagnosis.—*Rhamdia guasarensis* is distinguished from congeneric species by two characters: dorsal profile of head concave (Fig. 1, vs. convex or straight); and frontal bones broadly sutured to each other anterior to small, circular remnant foramen of anterior cranial fontanelle that is anteriorly adjacent to epiphyseal bar (Fig. 2, vs. frontals separated by anterior fontanelle widely
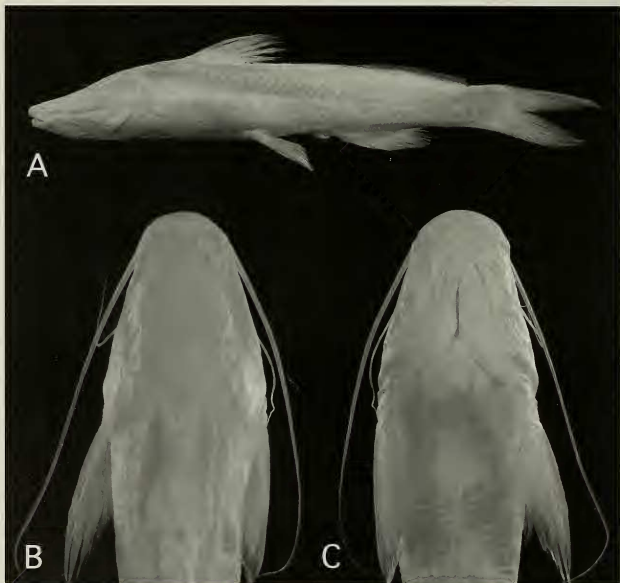
Fig. 1. *Rhamdia guasarensis.* Holotype MBUCV-V-29604, 106.8 mm SL. A, lateral view; B, dorsal view of head; C, ventral view of head.

open from mesethmoid to epiphyseal bar). *Rhamdia guasarensis* differs from all epigean *Rhamdia* by the following troglomorphic characters: absence of eyes, complete depigmentation, widened cutaneous pores of the cephalic laterosensory system, preoperculomandibular sensory canal forming wide fossae in the dentary and preopercle (Fig. 3, vs. narrow pores and canals).

In addition to these characteristics, *R. guasarensis* can be distinguished from other species of the genus by the following combination of characters: pectoral fins with a spine and ten branched rays (vs. modally

eight or nine soft rays in other species, data from Silfvergrip 1996); both lobes of the caudal fin pointed (vs. at least one lobe rounded); caudal skeleton with three hypural plates, PH; 1 + 2; 3 + 4 + 5 (vs. modally four PH; 1 + 2; 3 + 4; 5 in the other species with the exception of *R. laukidi* and *R. jequitinhonha,* see Silfvergrip 1996).

Description.—Morphometric data are presented in Table 1. Body elongate, strongly depressed anteriorly and gradually more compressed from origin of pectoral fins to caudal peduncle. Shape approximately tri-
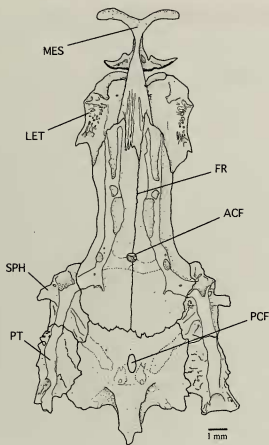
Fig. 2. *Rhamdia guasarensis*. Skull roof illustrating reduction of the anterior cranial fontanelle and midline contact of frontal bones. MBUCV-V-29622, 101.1 mm SL. Abbreviations: ACF, anterior cranial fontanelle; FR, frontal bone contact on midline; LET, lateral ethmoid; MES, mesethmoid; PCF, posterior cranial fontanelle; PT, pterotic; SPH, sphenotic.

Fig. 3. *Rhamdia guasarensis*. Enlarged preoperculomandibular laterosensory canal and associated foramina. MBUCV-V-29622, 101.1 mm SL. Abbreviations: ANG, anguloarticular; D, dentary; HYO, hyomandibula; MPT, metapterygoid; OP, opercle; POP, preopercle; Q, quadrate.

angular in transverse section at dorsal-fin origin. Dorsal profile sinusoidal anterior to dorsal fin, then approximately straight to middle of adipose fin, then slightly concave along caudal peduncle. Ventral profile nearly straight to anal-fin origin, then slightly concave posteriorly.

Head depressed, its dorsal profile concave, its lateral and ventral profiles nearly straight. Mouth terminal, upper jaw slightly in advance of lower jaw. Rictal folds little developed. Upper and lower lips with weak sulci, slightly evident in holotype, forming single labial fold. Premaxillaries with single band of diminutive teeth, arranged in ten irregular tooth rows, the posterolateral corn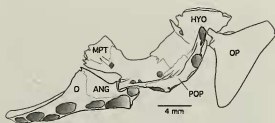ers rounded, not produced. Dentition of lower jaw similar to premaxillary teeth, in six irregular tooth rows. Palatine and vomer edentulous. Maxillary barbels long, extending beyond base of pelvic fins. Mental barbels relatively short, inner mentals scarcely reaching posterior border of branchial membrane; outer mentals surpass pectoral fin bases. Inner mental barbel bases inserted slightly in advance of outer mental barbel bases. Anterior nares tubular, near border of snout. Posterior nares with elongated orifices, bounded anterolaterally by membrane of fine skin. Internarial length less than width between posterior nares. Eyes completely absent. Branchial membranes overlapping medially; united to isthmus only anteriorly.

Cephalic lateralis sensory system with paired supraorbital (SO), infraorbital (IO), preopercular (POP), mandibular (MA), otic (OT), and post-otic (POT) canals, without tubular commissure connecting supraorbital canals. Sensory pores simple, not branched and multiple. SO canal with six pores: SO1–SO3 associated with nasal bone, SO1 medially adjacent to anterior naris, wide and delimited by membrane of fine skin, SO2 between anterior and posterior nares, slightly closer to first, SO3 posteromedially near posterior naris. SO4 near dorsal midline at end of short medial tube and separate from its counterpart of opposite side. SO5 lateral to its canal midway between SO4 and union of SO and IO canals. SO6 medial to its canal a little posterior to union of SO and IO canals.

Table 1.—Measurement data for the type series of *Rhamdia guasarensis*. Measurement 1 expressed in mm. Proportional measurements expressed as thousandths of standard length (2–19; 26–28) or head length (20–25).

	Holotype MBUCV-V-29604	Paratype MBUCV-V-29622	Paratype MBUCV-V-29622 (CS)	Paratype ANSP 179878
1. Standard length	106.8	87.2	101.1	93.4
2. Total length	1057	1093		1083
3. Body depth	162	178		167
4. Body width	171	180	168	173
5. Predorsal length	351	367	352	359
6. Preanal length	645	653	659	656
7. Prepelvic length	462	458		490
8. Preadipose length	555	545		530
9. Caudal peduncle length	211	210	214	224
10. Caudal peduncle depth	97	104		105
11. Dorsal fin spine length	85	86		108
12. Length of first branched dorsal fin ray	172	176	183	187
13. Dorsal fin base	115	121	104	113
14. Adipose fin length	387	411	432	394
15. Dorsal fin to adipose fin	99	72		68
16. Anal fin base	141	127	127	143
17. Pectoral fin spine length	121	111		123
18. Length of first branched pectoral fin ray	204	197	195	216
19. Pelvic fin length	169	153	159	169
20. Head length	259	262	256	276
21. Head width	661	645	631	633
22. Head depth	550	522	538	528
23. Internarial length	137	144		147
24. Anterior internarial width	173	169		187
25. Posterior internarial width	156	152		165
26. Maxillary barbel length	541	610	557	578
27. Outer mental barbel length	205	262	258	262
28. Inner mental barbel length	98	121	108	121

IO canal with four pores; IO1–3 wide like SO1. IO1 posterior to anterior nostril; IO2 emerges dorsal to groove for maxillary barbel, posterior to base of barbel; IO3 near point where IO canal curves dorsally; IO4 at tip of short posterior tube near union with SO canal. Holotype and one paratype (87.2 mm SL) have different single supernumerary IO pores; extra pore of holotype from left canal between the IO2 and IO3; extra pore of paratype from right IO canal between IO3 and IO4.

POP canal with four pores; MA canal with seven pores; all except MA1 and POP4 originate from much enlarged cavities in dentary and preopercular bones. MA1 in mental position near to midventral line at tip of its branch from lower jaw symphysis.

POT canal with two pores, POT1 over pterotic dorsal to gill opening; POT2 dorsal to supracleithrum and above main lateralis canal at level of first pore. First pore of lateralis canal at end of ventral branch dorsal to postcleithral process. Several following pores also at tips of short postero-ventral branches. Lateral line canal complete to base of middle upper-lobe caudal rays.

Dorsal fin with a spinelet, spine and six branched rays; its margin rounded. Dorsal spine weakly developed, only its basal part rigid and unsegmented; dentations diminutive and scarcely visible, limited to basal part of anterior margin. The distal two-thirds of dorsal spine flexible and obliquely segmented. Adipose fin long and low, its origin near tip of depressed dorsal fin, and extending posteriorly to approximately 80%
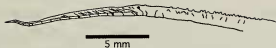
Fig. 4. *Rhamdia guasarensis.* Pectoral spine in dorsal view. Holotype MBUCV-V-29604, 106.8 mm SL.

of caudal peduncle length; posterior end of adipose fin adnate to caudal peduncle without a free fleshly tab. Caudal fin deeply forked; both caudal lobes pointed; upper lobe slightly longer than lower; membrane uniting innermost caudal rays complete. Principal caudal rays i,7-8,i, except i,7-7,i in one paratype. Anal fin with 12 rays, anteriormost two or three rays simple, others branched; its margin rounded.

Pectoral fins with a spine and ten branched rays. Pectoral spine (Fig. 4) with weak dentations proximally on anterior margin; distal half of spine flexible and obliquely segmented. First branched pectoral-fin ray longest, posterior branched rays diminishing in length. Postcleithral process short, sharp. Pelvic fins with one simple ray and five branched rays, its origin posterior to end of dorsal fin.

Skull roof (Fig. 2) with anterior cranial fontanelle extremely reduced to a small circular foramen located in front of epiphysial bar; mesethmoid posteriorly lacking concave notch of fontanelle, and frontals meeting medially along most of their length. Posterior cranial fontanelle reduced to oval foramen near center of supraoccipital. Supraoccipital process short, its length about equal to length of supraoccipital body.

Anus and urogenital papillae separated, anus located equidistant between medial edge of pelvic-fin base and urogenital papilla, approximately at midlength along pelvic fins; urogenital papilla conspicuous and elongated, located closer to base of anal fin than to base of pelvic fins.

Total vertebrae 40–42; neural spines of vertebrae 6–10 bifid; hemal arch closed in vertebra 12 or 13, first hemal spine on vertebra 14, 15 or 16; eight pairs of ribs borne on vertebrae 6–13. Seven dorsal-fin ptery-

Fig. 5. The Lago de Maracaibo—Sierra de Perijá region, Venezuela, showing type locality (star) of *Rhamdia guasarensis.* Map based on shaded relief image PIA03388, Shuttle Radar Topography Mission, National Aeronautics and Space Administration (NASA).

giophores preceded by small supraneural; first dorsal-fin pterygiophore inserted between rami of neural spine of fourth vertebra. Eleven anal-fin pterygiophores, first inserting posterior to hemal spine of vertebra 21. Caudal skeleton with three hypural plates: rectangular parhypural; triangular hypurals 1 + 2; triangular hypurals 3 + 4 + 5.

Color in alcohol.—Body and fins completely depigmented; most of skin, rayed- and adipose-fin membranes hyaline and translucent; musculature appearing yellowish, particularly jaw adductors and dorsal trunk myomeres; parts of head and fin bases whitish.

Distribution and habitat.—*R. guasarensis* is known only from the Surgencia del Tigre (Zu. 23), in the middle basin of the Río Guasare, north of the Sierra de Perijá in northwestern Venezuela (Fig. 5). The cave is near the margin of Río Guasare and is the source of a spring during seasonal rains (Sociedad Venezolana de Espeleología

1991). The cave's lower conduit has a 280 m course, 2–3 m wide and 1–2 m high, narrowly communicating with the access gallery. The underground river is permanently fed by a spring about 60 m into the lower gallery. At the time the cave was surveyed, the average depth of this water course was 1.5 m with deeper pools along its course where the catfishes were observed (Sociedad Venezolana de Espeleología 1991).

Etymology.—The name is based on Río Guasare, parent stream of the subterranean waters in which this endemic catfish species lives.

Discussion

Rhamdia guasarensis is placed in Heptapteridae by its possession of four synapomorphies identified for the family (Lundberg & McDade 1986, Ferraris 1988, Bockmann & Guazelli 2003): posterior limb of fourth transverse process expanded and notched; posterodorsal corner of hyomandibula greatly expanded for attachment of levator operculi muscle; dorsal margin of quadrate free, not sutured to hyomandibula and metapterygoid; ventrolateral corner of mesethmoid anteriorly recurved. However, the new species lacks a fifth synapomorphy of heptapterids: a straight-edged vertical bony lamina on the Weberian complex centrum. Instead, the vertical lamina has a concave margin in *R. guasarensis.*

Except for the obvious lack of a free orbital rim, *R. guasarensis* possesses the character combination presented as diagnostic of *Rhamdia* by Silfvergrip (1996:74). This includes: three pairs of barbels, double lip fold, vomer without teeth, transverse processes of fourth vertebra expanded branched distally, supraoccipital process not contacting anterior nuchal plate, adipose fin with free posterior margin, posterior fontanelle closed and postcleithral process well developed. However, none of these are unambiguous synapomorphies of the group of species comprising *Rhamdia.* Instead, some characters are heptapterid or

higher level synapomorphies, and others, some of uncertain polarity, have wider and variable distributions among heptapterids. Thus, placement of this new species in *Rhamdia* must be considered provisional because the genus has not been supported as monophyletic. Bockmann's (1998) phylogenetic analysis of Heptapteridae placed one representative species, *R. laticauda,* sister to *Pimelodella* but a second species, *R. quelen,* is deeper in his cladograms. In this context *R. guasarensis* has one derived, although non-unique, feature listed by Bockmann as diagnostic for *R. quelen.* This is the highly reduced posterior cranial fontanelle, long used as one of the diagnostic characters of *Rhamdia.* Indeed, we find the posterior fontanelle closed or reduced to a small foramen in the supraoccipital in most other *Rhamdia* examined: *R. laukidi, R. nicaraguensis, R. quelen* (including specimens originally identified as *R. guatemalensis, R. hilarii, R.vilsoni, R. wagneri*) and some *R. laticauda.* Silfvergrip (1996) reported the fontanelle to be variably open or reduced in *R. laticauda,* and our sample also shows such variability among specimens. We find that *R. muelleri* has an open posterior fontanelle. The fontanelle is also closed in the heptapterids *Brachyglanis, Brachyrhamdia, Leptorhamdia,* and *Myoglanis* (Bockmann 1998, pers. obs.). Furthermore, *R. guasarensis* has an uncinate process on hypobranchial 1, unlike *R. quelen* that lacks the process (listed as a second non-unique derived feature of *R. quelen* by Bockmann 1998). Accordingly, we do not take the foregoing as evidence for a particularly close phylogenetic relationship between *R. guasarensis* and *R. quelen.* The midline union of frontal bones (Fig. 2) and concomitant extreme reduction of the anterior fontanelle are a distinctive apomorphic character of *R. guasarensis.* Although not all species have been examined for this feature, we have not observed it in any *Rhamdia* nor has it been previously reported, and in his description of the genus, Silvergrip (1996:74) reported the anterior fontanelle to

be invariably open. This is at least a diagnostic autapomorphy of the species, although these features are potentially informative about relationships. Bockmann (1998) illustrated a variety of conditions of anterior fontanelle narrowing and closure in other heptapterids including *Myoglanis, Taunayia, Imparfinis pristos,* and an undescribed species, but all of these are structurally different from that in *R. guasarensis.*

Another peculiar character of the new species is the concave dorsal profile of the head. In general, *Rhamdia* species, including most cave populations, have convexly rounded heads. The cave species *R. macuspanensis* recently described from Mexico (Weber & Wilkens 1998) has a straight dorsal head profile, somewhat more similar to that of *R. guasarensis* than to other congeners. *Rhamdia macuspanensis* is readily distinguished from *R. guasarensis* by its strong development of pectoral spine dentations and rounded tips of the caudal lobes.

Rhamdia guasarensis possesses typical reductive characteristics in common with other cave-dwelling species and populations of the genus. Furthermore, the greater relative length of the head and elevated number of pectoral-fin rays are also shared by other troglobitic species of the genus (Weber 1996). It has been suggested that larger head size is related to an increase in the development of the cephalic laterosensory system (Langecker & Longley 1993, Weber 1996), and the greater number of pectoral-fin rays is possibly correlated with the increased mass of the anterior part of the body, compensating this increase with a greater fin area for hydrodynamic lift (Weber 1996). If there is a functional relationship between head size and pectoral-fin area in cave dwelling *Rhamdia,* it does not extend to the heptapterid genus *Pimelodella,* wherein the large-headed *P. kronei* has eight or nine pectoral-fin rays (Trajano 1997, Trajano & Britski 1992) and the small-headed *P. spelaea* has ten pectoral-fin rays (Trajano et al. 2004).

No *Rhamdia* species are known from the surface waters of Río Guasare, thus *R. guasarensis* is not a cave-dwelling ecotype of a proximate epigean species. Two *Rhamdia* species have been reported from northwestern Venezuela. From the Lago de Maracaibo Basin, Schultz (1944) published on specimens now identified as *R. quelen* (Silfvergrip 1996). Fernández-Yépez & Martín (1953) reported *R. wagneri* based on specimens collected in the Río Negro in the southern part of the Perijá range. One of us (CDN) has reidentified these specimens at the Museo de Historia Natural La Salle as *R. quelen.* As noted above, there is no evidence for a uniquely close relationship between *R. guasarensis* and *R. quelen.*

The fauna of troglobitic catfishes of the Sierra de Perijá region includes: *Ancistrus galani* Pérez & Viloria, 1994, *Trichomycterus spelaeus* DoNascimiento, Villarreal & Provenzano, 2001, and *Rhamdia guasarensis.* There is another hypogean population of *Trichomycterus,* possibly an undescribed species, living in a cave drained by the Río Yasa (Río Negro system) in the southern part of the Sierra de Perijá (DoNascimiento, in prep.).

The diversity of three cave catfishes of the Río Guasare system is among the highest of any Neotropical karst region, although the species are not found syntopically in the same cave. By contrast Bichuette & Trajano (2003) list five troglobitic species in caves of the São Domingos karst area, Goiás, Brazil. *Ancistrus cryptophthalmus* and the trichomycterid *Ituglanis passensis* coexist in the São Vicente cave, Tocantins Basin, Goiás, Brazil (Trajano & Souza 1994, Fernández & Bichuette 2002). Also, the inundated caves of the Formosinho karst region of Bodoquena, Mato Grosso do Sul, southeastern Brazil, are co-inhabited by *Ancistrus formoso* and an undescribed troglomorphic population of *Trichomycterus* (Sabino & Trajano 1997).

Cave-dwelling and specialized troglobitic neotropical catfishes belong to the families Astroblepidae, Heptapteridae, Loricariidae, and Trichomycteridae. Within the last three

of these families the genera *Rhamdia, Ancistrus,* and *Trichomycterus* are most commonly represented in cave faunas. Their prevalence suggests possession of morphological, physiological, behavioral, and ecological features (preadaptations) that facilitate existence in cave waters (Eigenmann 1919, Norman 1926, Hubbs 1936).

Wilkens (1986) proposed a correlation between degree of morphological reduction and time of subterranean evolution based on a neutral mutation model for the regressive evolution of eyes and pigmentation in cave fishes and crustaceans. The subterranean catfishes of the Sierra de Perijá, especially *Trichomycterus spelaeus* and *R. guasarensis,* are highly advanced in their troglobitic features, suggesting that they are not new arrivals in their subterranean environment. Ocular and pigmentation reduction of *R. guasarensis* and *T. spelaeus* are complete. These species exhibit additional autapomorphies such as extremely elongate barbels in *Trichomycterus* and much enlarged head laterosensory organs in *Rhamdia.* These characters, too, may indicate a long period of hypogean evolution. Indirect evidence suggests the availability of an ample period of time for the evolution of the Perijá cave fishes. Paleogeographic reconstructions of northwestern Venezuela suggest that uplift of the Sierra began in the early Cenozoic (González de Juana et al. 1980). It is reasonable to assume that these fishes originated in situ after subterranean waters carved out their habitat within Cretaceous limestones of the Sierra de Perijá. On the fish side of the equation, the only fossil record of *Rhamdia* are fin spines of relatively young Pleistocene age (Cione 1982). However, based on much older Miocene fossils of phylogenetically related pimelodid and pseudopimelodid catfishes, the heptapterids are expected to have originated and diversified long before the late Pleistocene (Lundberg 1998). Thus it is possible that subterranean aquatic habitats and cave fishes have been present in this region for tens of millions of years.

Comparative material.—*Rhamdia laticauda*: ANSP 104034, one specimen, X-ray and alc, 86 mm SL, Panama, Cocle; UMMZ 197078, two dry skeletons, 131–146 mm SL, Honduras. *R. laukidi*: ANSP 139184, one of three specimens, X-ray and alc, 127 mm SL, Colombia, Meta. *R. muelleri*: ANSP 162521, two of four specimens, X-ray and alc, 109–110 mm SL, Venezuela, Amazonas. *R. nicaraguensis*: ANSP 8444, one specimen, alc, 135 mm SL, Nicaragua, Lago Nicaragua. *Rhamdia quelen*: ANSP 141578, two of five specimens, X-ray and alc, 100–105 mm SL, Venezuela, Bolívar; ANSP 45365 (original identification *R. guatemalensis*), one specimen, X-ray and alc, 120 mm SL, Panama, Canal Zone; ANSP 172138 (original identification *R. hilarii*), two of 37 specimens, X-ray and alc, 107–110 mm SL, Brazil, Minas Gerais; ANSP 16020 (original identification *R. vilsoni*), one specimen, alc, 200 mm SL, Trinidad; ANSP 71621 (original identification *R. wagneri*), one specimen, X-ray and alc, 125 mm SL, Colombia, Magdalena; DU-F1021, one dry skeleton, 202 mm SL; MBUCV-CT-561, eight specimens, CS, 23–57 mm SL, Venezuela, Zulia; MHNLS-1645, two specimens, alc, 59–223 mm SL, MHNLS-1734, three specimens, alc, 107–228 mm SL, Venezuela, Zulia.

Acknowledgments

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